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Research Article

The alien conifer *Cupressus arizonica* can outcompete native pines in Mediterranean mixed forests under climate change

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Abstract

Exotic species have been introduced in afforestation and reforestation initiatives worldwide. Climate change, including increased aridity and extreme events, can promote the spread of exotic species used in forest plantations while hampering the performance of natives. Evaluating whether climate change may affect the success of biological invasions is key to project dominance shifts in forest ecosystems, yet it requires a comprehensive approach that integrates main demographic rates driving tree population dynamics. Here, we evaluated the performance of co-occurring native pine species (*Pinus pinaster*, *P. nigra* and *P. sylvestris*) and the exotic *Cupressus arizonica* in mixed forests in Mediterranean mountains by comparing their main demographic rates (regeneration, mortality and growth) and radial growth response to extreme droughts and to climate change scenarios. Overall, the exotic *C. arizonica* showed less growth dependence to climatic variability, higher growth resilience to drought, lower mortality and higher regeneration capacity than *P. sylvestris* and *P. pinaster*. However, *P. nigra* showed higher regeneration and similar growth response to extreme droughts than *C. arizonica*. In addition, growth models pointed to better performance of the exotic species under future climate change scenarios than co-occurring natives. Our results suggest that *C. arizonica* can increase its dominance (relative presence within the forest area), which can enhance its invasive potential and range expansion. Thus, attention is needed to better control the invasive potential of this exotic species in Mediterranean forest ecosystems.

Key words: Biological invasions, climatic scenarios, dendroecology, drought, forest dynamics, global change, invasiveness, resilience

Introduction

Understanding interactive effects between different global change drivers is key to forecast their impacts on ecosystems (IPBES 2019). Biological invasions and climate change are major drivers of global environmental change, threatening biodiversity and ecosystem functions worldwide (Vitousek et al. 1997; Butchart et al. 2010; IPBES 2023; IPCC 2023). However, assessing how climate change affects the success of biological invasions remains challenging (Cosner 2014; Hulme 2017). Ongoing climate change could favour the colonisation, persistence and

spread of early successional species in disturbed ecosystems, as is the case of many invasive plant species (Dukes and Mooney 1999; Lenoir et al. 2008). Under climate change, invasive plant species may obtain even more advantage from their greater capacity for carbon gain, higher performance over a wide range of resource availabilities and higher phenotypic plasticity than native species (Davidson et al. 2011; Godoy et al. 2011). Thus, climate change might promote the colonisation of these species by increasing their invasiveness while hampering the performance of natives (Dukes and Mooney 1999; Hellmann et al. 2008; Huang et al. 2011). However, several studies reported a wide range of species-specific and context-dependent responses, calling for further investigations on climate change effects on the performance of co-occurring native and invasive species (Diez et al. 2012; González-Muñoz et al. 2014; Medina-Villar et al. 2020).

Plant species are not only experiencing gradual changes in average climate conditions, but also a higher frequency and intensity of extreme climatic events, such as droughts and heat waves that severely impact Mediterranean ecosystems (Spinoni et al. 2018; IPCC 2023; Toreti et al. 2024). Extreme droughts impose severe stressful conditions on native plant species, which, in turn, could reduce their competitive ability and resistance to invasions. This can prompt the establishment and spread of invasive species populations with greater tolerance to new environmental conditions (Stromberg 1998; Kane et al. 2011). In forest ecosystems, extreme droughts can even exceed the ecophysiological tolerance of native canopy-dominant species, triggering widespread tree mortality (Allen et al. 2015), which implies large releases of resources (e.g. light, water) that could favour the establishment of early successional invasive species (Kane et al. 2011; Diez et al. 2012). The duration of the invasion window after a given disturbance (e.g. extreme climatic event) depends not only on the local environmental conditions (e.g. water, temperature) for the germination and growth of the colonising exotic species (Jastrzębowski et al. 2021; Orbán et al. 2021; Klisz et al. 2023), but largely on the resilience capacity of native species (Diez et al. 2012). Therefore, evaluating the resilience capacity to extreme droughts of co-occurring native and exotic tree species could be used to forecast near-future invasions in drought-prone ecosystems, such as those in Mediterranean and semi-arid regions.

Many exotic tree species have been planted throughout the world's forests in plantations or reforestations, some of which have been successfully naturalised and/or become invasive (Richardson and Higgins 1998; Mortenson and Mack 2006; Vítková et al. 2017; Dimitrova et al. 2022; FAO 2022). The invasiveness of these exotic tree species can be increased by improved performance due to beneficial climatic changes (e.g. warming, Scholze et al. (2006)) and/or by reduced competition during extremely adverse climatic conditions because of higher resilience than co-occurring native species (Olano and Palmer 2003; Suarez and Kitzberger 2010). Recent studies using species distribution models (SDMs) have predicted distributional range shifts of exotic tree species under climate change in Europe (Puchałka et al. 2020, 2023). However, studying species-specific responses to climatic trends and extremes, such as drought events, at local scales is crucial to understand acclimatisation responses of native and non-native tree species (Klisz et al. 2023).

Tree growth is one of the main demographic parameters determining population dynamics along with mortality and regeneration capacity, which are critical to evaluate the invasive capacity of a given exotic tree species. The quantification

of tree growth through tree ring measurements has been used to assess the performance of co-occurring exotic and native tree species (Mortenson and Mack 2006; Mácová 2008; Vanhellemont et al. 2011; González-Muñoz et al. 2015). Tree ring-width series allow us to evaluate growth responses to past and current climatic variability and to analyse growth resilience to extreme climatic events (Fritts 1976; Lloret et al. 2011). Further, ring-width series could be used to forecast growth responses to projected climate changes (e.g. González-Muñoz et al. (2014); Matías et al. (2017)). However, few studies have compared the response of co-occurring native and exotic tree species to projected climatic changes (but see: González-Muñoz et al. (2014)). Thus, the analysis of growth responses to current and projected climate in co-occurring native and exotic tree species, coupled with the evaluation of growth resilience to current extreme climatic events, may contribute to assess potential changes in species performance and subsequent shifts in forest species dominance. In addition, regeneration capacity and background mortality of co-occurring native and exotic species could play a critical role in native-exotic species dynamics. To the best of our knowledge, there is a lack of studies that evaluated the performance of co-occurring native and exotic species following such an integrative approach.

In Mediterranean mountains, native pine species are spatially segregated along environmental and altitudinal gradients according to their drought-tolerance (Ruiz-Benito et al. 2012). In some forest areas, native pine species co-occur with the exotic *Cupressus arizonica* Greene., an evergreen conifer native to North America adapted to dry and cold conditions and widely planted out of its native range (Flora of North America Editorial Committee 1993; CABI 2020). In southern Europe (e.g. Spain, North Macedonia), *C. arizonica* was used in afforestation/reforestation and for soil protection since ca. mid-twentieth century (Dimitrova et al. 2022). Although *C. arizonica* is not currently considered as invasive species in these areas, it was able to escape plantations and become a naturalised species (Sanz Elorza et al. 2004). However, it was reported as an invasive species in other areas, such as in Hawaii (Swearingen and Bargeron 2016). On average, exotic trees introduced to Europe can become invasive after 170 years from introduction (Kowarik 1995). In the case of *C. arizonica*, this lag time could be reduced under future climate changes, in which drier conditions could favour the performance of this species over that of the native pine species. However, the ability of this exotic species to spread and invade Mediterranean ecosystems has not been explored yet. This information is essential for the management of established exotic species. In fact, the European Regulation 1143/2014 on invasive alien species established the need to identify potential invasive alien species of European concern, i.e. those likely to arrive, establish, spread and have an impact on native biodiversity or associated ecosystem services in Europe.

Therefore, our main objective was to compare tree performance of co-occurring native pines (*P. sylvestris*, *P. nigra* and *P. pinaster*) and exotic species (*C. arizonica*) along altitudinal vegetation belts in mixed conifer forests of the central Iberian Peninsula. The specific objectives of the present study were: i) to quantify regeneration capacity and mortality of both native and exotic species; ii) to compare growth-climate relationships between co-existing native and exotic species; iii) to compare components of tree growth resilience in response to extreme drought events between native and exotic species; and iv) to forecast species growth throughout the 21st century under different climate change scenarios. Given species-specific

tolerances to drought and their biogeographic origin, we expected that the exotic *C. arizonica* will show lower growth sensitivity to water availability, higher growth resilience to extreme droughts and higher regeneration and lower mortality than *P. nigra* and *P. sylvestris*, but similar to *P. pinaster*. Accordingly, we hypothesised more severe growth declines in the next century for *P. nigra* and *P. sylvestris* compared to *C. arizonica* due to projected increased aridity.

Methods

Study area

The study area is located in La Pedriza, a large granite complex located on the south face of the Sierra de Guadarrama National Park in the central Iberian Peninsula (40°44'N, 3°54'W). La Pedriza comprises about 3,200 ha and ranges from 890 to 2,090 m a.s.l. The climate is continental Mediterranean with cold winters and dry summers. Mean annual precipitation and mean annual temperature are 533 mm and 11.7 °C, respectively (period 1974–2018, data from the nearest meteorological station of the Spanish National Agency for Meteorology "Colmenar Viejo", 15 km away from the study area at 1,004 m a.s.l.). Soils are classified as district Cambisol and Leptosol over a granitic substrate (IUSS Working Group WRB 2015). The study area is dominated by pine forests of several species that are distributed at different altitudes. *P. pinaster* is the dominant tree species at low elevation stands (about 900–1,200 m a.s.l.), whereas mid-high elevation stands are dominated by *P. nigra* (about 1,100–1,300 m a.s.l.) and *P. sylvestris* (about 1,100–1,800 m a.s.l.). Most of these forests originated from afforestation/reforestation programmes between 1940 and 1970. Understorey vegetation is mainly composed of *Cistus ladanifer* L., *C. laurifolius* L., *Juniperus oxycedrus* L. and *J. thurifera* L., amongst others. *Quercus ilex* L. and *Q. pyrenaica* Willd. appear as secondary tree species in some areas.

In this area, *Cupressus arizonica* appears in monospecific stands and mixed with pine species between 900 and 1,300 m a.s.l as the result of afforestation programmes for erosion control between 1960 and 1970 (Valdés and Carlos 1996). In its native range, it occurs in a wide range of soil types at elevations between 1,000 and 2,000 m a.s.l., with an annual precipitation between 400 and 600 mm (Flora of North America Editorial Committee 1993).

Sampling design and dendroecological methods

Within the study area, we randomly selected forest stands where *Cupressus arizonica* co-occurred with one of the three study pine species. We selected three stands for each mixed forest type (i.e. species combination): *C. arizonica* - *Pinus pinaster* (CP), *C. arizonica* - *P. nigra* (CN) and *C. arizonica* - *P. sylvestris* (CS). CP stands ranged in altitude between 950 and 1150 m a.s.l, in density between 350 and 500 trees ha^{-1} and in basal area between 29.3 and 39.7 m^2 ha^{-1} (Suppl. material 1: table S1). CN stands were sampled at altitudes between 1090 and 1250 m a.s.l, showed tree density between 333 and 800 trees ha^{-1} and had basal area between 32.9 and 76.6 m^2 ha^{-1}. CS stands ranged in altitude between 1130 and 1270 m a.s.l, in density between 400 and 1233 trees ha^{-1} and in basal area between 69.4 and 70.0 m^2 ha^{-1} (Suppl. material 1: table S1).

At each stand, we randomly established two independent 30 × 10 m transects and recorded the diameter at breast height (DBH), species identity and the number of dead trees. To quantify the regeneration capacity of the studied species, we recorded the presence and species identity of tree seedlings (height < 50 cm) in 10 circular plots of 5 m radius randomly distributed at each forest stand.

We randomly selected at each stand five dominant or co-dominant trees of each species for dendroecological analyses, which resulted in 15 trees per species at each mixed forest type. We recorded the DBH of each target tree and sampled two wood cores at breast height using a Pressler increment borer. Wood cores were air-dried, glued on wooden supports and polished using sandpapers of progressively finer grain. Tree growth series were visually cross-dated using pointer years (Yamaguchi 1991). We used mean inter-series correlation (Rbar) and expressed population signal (EPS) to evaluate the strength of the common growth signal amongst sampled trees (Wigley et al. 1984). Rbar and EPS were 0.38 and 0.92, respectively, suggesting a strong common signal of analysed growth series. First order autocorrelation (AR1) was 0.61. Rbar, EPS and AR1 were calculated using dplR (Bunn 2010). Samples were then scanned at 1,200 dpi resolution (EPSON V8 Perfection) and tree ring width was measured to the nearest 0.01 mm using ImageJ (Schneider et al. 2012). Tree annual growth was quantified as basal area increment (BAI, cm^2), following Biondi and Qeadan (2008):

$$BAI = \pi(r_t^2 - r_{t-1}^2)$$

where r_t and r_{t-1} are the stem radius at the end and at the beginning of a given annual ring, respectively. Sampled trees of *C. arizonica* and pines showed similar BAI and age at breast height, but *P. pinaster* and *P. nigra* were significantly greater in DBH than *C. arizonica* (Suppl. material 1: table S2). Despite the oldest tree dated to 1939, we selected 1974–2018 as the study period to maximise sample size for statistical analyses and using the threshold value for EPS of 0.85.

Climatic data

Monthly climatic data (mean temperatures and total precipitation) for the study period (1974–2018) were obtained from Colmenar Viejo meteorological station (Spanish Meteorological Agency, 30 km from the study area). Water balance (P-PET) was calculated as the difference between precipitation (P) and potential evapotranspiration (PET). PET was calculated following Thornthwaite (1948). For each year, we calculated annual mean temperature (T), total precipitation (P) and water balance from October of the previous year to September of the target year. Previous autumn and winter precipitations can play an important role in recharging soil water reserves, thereby influencing current year radial growth in conifers (Sánchez-Salguero et al. 2012; Madrigal-González et al. 2018). Mean temperature and total precipitation were also seasonally calculated: mean temperature and total precipitation of the previous autumn (October to December; Tau and Pau, respectively), current winter (January to March; Twi and Pwi, respectively), current spring (April to June; Tsp and Psp, respectively) and current summer (July to September; Tsu and Psu, respectively). The use of seasonal climatic variables instead of monthly ones allowed the creation of more parsimonious growth models, while maintaining a reliable representation of climatic trends (Matías et al. 2017).

Climatic data for the study area during the period 1974–2100 were obtained from the CRU database (Climate Research Unit, University of East Anglia). Climatic data are projected according with the CMIP5 - Coupled Model Intercomparison Project (Taylor et al. 2012) under the RCP2.6 and RCP8.5 forcing scenarios from IPCC (2013). These scenarios are based on stringent mitigation measures and on no additional efforts to constrain emissions, respectively. Climate scenarios project an increase in mean annual temperature of 1.2 and 4.7 °C for RCP2.6 and RCP8.5, respectively, by the end of the 21st century (2080–2100) compared to the study period (1974–2018). Annual precipitation is expected to decrease by 8 and 139 mm for RCP2.6 and RCP8.5, respectively. Projected seasonal mean temperature and precipitation were calculated as for data from the meteorological station. For the study period (1974–2018), the mean temperature and total precipitation from CRU database and the nearest meteorological station to the study area were significantly correlated ($P < 0.001$; r = 0.88 and r = 0.72, respectively).

Data analysis

Growth-climate relationships

We fitted a growth model for each pine species (*P. pinaster*, *P. nigra* and *P. sylvestris*) and three growth models for *C. arizonica*, one for each mixed forest type (i.e. CP, CN and CS). Following the procedure by Fajardo and McIntire (2012), we evaluated climate-growth relationships by fitting generalised additive mixed effect models using the *gam* function in the *gamm4* package (Wood and Scheipl 2017). The response variable (i.e. BAI) was log-transformed to achieve homoscedasticity. We considered tree identity nested within forest stands as the random term in the model to account for non-independence amongst observations within the same tree (i.e. repeated measurements) and within the same forest stand. We also used an autoregressive correlation structure to remove the first-order autocorrelation between observations of consecutive years (Pinheiro et al. 2018). We considered as fixed effects tree age as a smooth spline (with default package settings) and the eight seasonal climatic variables (Tau, Twi, Tsp, Tsu, Pau, Pwi, Psp and Psu) as linear effects. Climatic variables were standardised (i.e. the mean was subtracted from each value and divided by the standard deviation) to allow comparisons across model-estimated parameters (Zuur et al. 2009). To identify the best-supported model, we fitted all potential models and selected the one that minimises the Akaike's Information Criterion corrected for small samples (AICc). Potential models were fitted by the Maximum Likelihood method using the *dredge* package (Barton 2018). The parameters of the selected model were obtained by Restricted Maximum Likelihood (Zuur et al. 2009). We evaluated species' BAI trend for the period 1974–2018 by fitting a linear model per mixed forest type and considering the interaction between species and year as fixed effects. All statistical analyses were done in R v.3.5.3. (R Core Team 2019).

Tree growth response to extreme drought events

We identified drought events as those years with annual P-PET below the 15th percentile of the P-PET series (Muñoz-Gálvez et al. 2021). We identified 1991, 1995,

2005 and 2012 years as drought events in the study period. For each drought event, we evaluated growth resistance, recovery and resilience for each sampled tree following Lloret et al. (2011):

$$Resistance\ (Rt) = Dr\ /\ PreDr$$

$$Recovery\ (Rc) = PostDr\ /\ Dr$$

$$Resilience\ (Rs) = PostDr\ /\ PreDr$$

where *PreDr* was the mean BAI before the drought event; *Dr* was the BAI the year of the drought; and *PostDr* was the mean BAI after the drought. We calculated these indices considering pre- and post-drought periods of three years (Marqués et al. 2016; Andivia et al. 2020).

We used linear mixed models (LMM) to evaluate inter-specific differences in growth resilience to extreme droughts for each mixed forest type. We fitted an LMM for each pair of species and resilience component (i.e. resistance, resilience and recovery) using the R package *nlme* (Pinheiro et al. 2018). Resistance, recovery and resilience indices were log-transformed to achieve homoscedasticity. We considered tree identity nested within forest stands as the random term in the model to account for non-independence amongst observations within the same tree (i.e. repeated measurements due to the evaluation of different drought events) and within the same forest stand. Species identity was considered as a fixed effect in the model. The DBH of the individuals in the year of the drought event was included as a covariate (Andivia et al. 2020). We also considered as covariates the relative intensity of the drought event, expressed as the P-PET value during the drought and the difference in P-PET between the periods considered to the calculation of the growth resilience indices (DeSoto et al. 2020).

Forecasting species growth under different climate change scenarios

To forecast tree growth for the period 2019–2100, we followed the procedure by González-Muñoz et al. (2014) and Matías et al. (2017). The best-supported growth models in section *Growth-climate relationships* were run to forecast the BAI of each species and mixed forest for the periods 2019–2048, 2049–2078 and 2079–2100 under the RCP2.6 and RCP8.5 climatic scenarios. For each period and mixed forest, we simulated the annual BAI of 1000 individuals per species and stand (i.e. three simulations per species for each mixed forest type) with initial ages at breast height randomly distributed between those values that allow the restriction of simulations to the age range of sampled trees (Matías et al. 2017). Finally, we evaluated the predicted species' BAI trend for each simulated period by fitting a linear model per mixed forest type and climatic scenario and considering the interaction between species and year as fixed effects.

Results

Regeneration capacity and tree mortality

Seedling density of all species was rather low, ranging from 0 to 63.7 ± 33.7 ind/ha. *Cupressus arizonica* showed higher regeneration than co-occurring pines at CP (8.5 ± 4.2 vs. 0 ind/ha, for *C. arizonica* and pine species, respectively) and CS

stands (63.7 ± 33.7 vs. 12.7 ± 7.4 ind/ha). However, at CN stands, *Pinus nigra* showed higher regeneration than *C. arizonica* (21.2 ± 11.2 vs. 12.7 ± 12.7 ind/ha). Native *Juniperus oxycedrus* and *Quercus ilex* seedlings were present in all the sampled stands, showing values between 12.7 ± 7.4 and 67.9 ± 11.2 ind/ha for *J. oxycedrus* and between 46.68 ± 27.8 and 89.1 ± 32.1 ind/ha for *Q. ilex*. Regarding tree mortality, we found that 8.9% and 10% of the *P. pinaster* and *P. sylvestris* trees in the sampled stands were dead, respectively. *P. nigra* showed lower mortality rate (2.7%), whereas no *C. arizonica* trees were dead.

Growth trend and climate-growth relationships

We found contrasting growth trends between *Cupressus arizonica* and *Pinus pinaster* and *P. sylvestris* (Fig. 1). In CP stands, *C. arizonica* showed a significant positive BAI trend over the study period (i.e. 1974–2018; slope ± SE, 0.33 ± 0.03; $p < 0.05$), whereas *P. pinaster* showed neutral (i.e. non-significant) growth trend (0.01 ± 0.04). *C. arizonica* and *P. nigra* showed neutral growth trend in CN stands (-0.07 ± 0.04 and 0.05 ± 0.04, respectively). In CS stands, *P. sylvestris* showed a significant negative BAI trend (-0.24 ± 0.03), whereas *C. arizonica* showed a neutral growth trend over the study period (-0.04 ± 0.04).

Climatic drivers of tree growth were different for *C. arizonica* and co-occurring pine species (Table 1; Suppl. material 1: table S3). Pine species growth was more sensitive to climatic factors than *C. arizonica* (i.e. absolute values of regression coefficients were higher and more climatic variables explained the growth of pines and, thus, were selected in the models, Table 1). In CP stands, the growth of both species was positively related to spring and summer temperatures and to winter and spring precipitations. The growth of *P. pinaster* was also positively related to autumn and winter temperatures and to summer precipitation. In CN stands, the growth of *C. arizonica* only showed a positive response to winter temperatures and summer precipitation, while the growth of *P. nigra* was positively related to winter and spring temperatures and to precipitations from winter to summer (Table 1). In CS stands, the growth of *C. arizonica* was only related to winter temperatures,

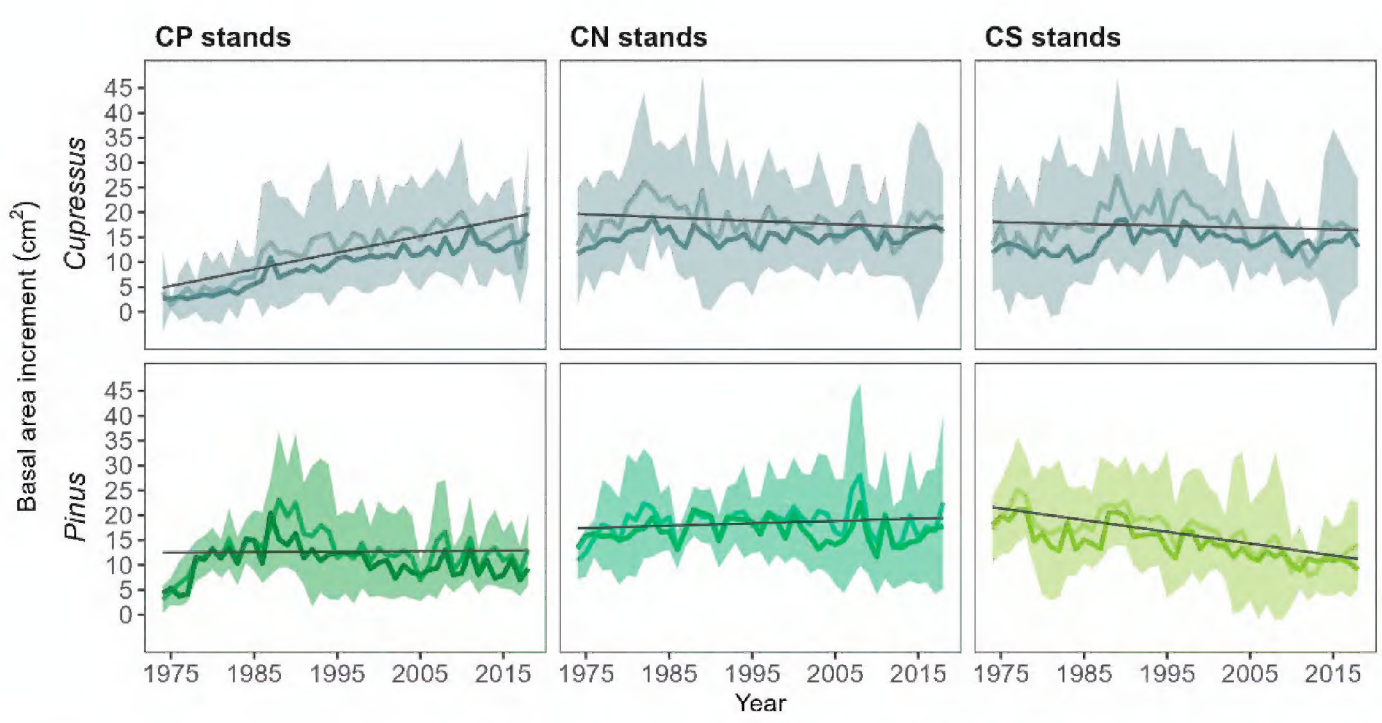

Figure 1. Mean observed (± SD; light colours) and predicted basal area increment (dark colours) over the period 1974–2018 for each mixed forest type and species. Black lines represent growth trends for the study period. CP: *Cupressus arizonica* and *Pinus pinaster* mixed stands; CN: *C. arizonica* and *P. nigra* mixed stands; CS: *C. arizonica* and *P. sylvestris* mixed stands.

Table 1. Regression coefficients (± SE) of the selected tree growth model for each mixed forest type and species.

	CP stands		CN stands		CS stands	
	C. arizonica	*P. pinaster*	*C. arizonica*	*P. nigra*	*C. arizonica*	*P. sylvestris*
Tau		0.08 ± 0.03				
Twi		0.12 ± 0.04	0.08 ± 0.03	0.13 ± 0.03	0.11 ± 0.03	0.10 ± 0.03
Tsp	0.16 ± 0.05	0.18 ± 0.05		0.08 ± 0.04		-0.16 ± 0.03
Tsu	0.06 ± 0.04	0.17 ± 0.03				
Pau						
Pwi	0.08 ± 0.04	0.18 ± 0.04		0.05 ± 0.03		0.05 ± 0.03
Psp	0.11 ± 0.04	0.16 ± 0.04		0.08 ± 0.03		0.08 ± 0.03
Psu		0.13 ± 0.03	0.06 ± 0.03	0.10 ± 0.02		
R^2	0.401	0.287	0.369	0.363	0.369	0.352

CP: *Cupressus arizonica* and *Pinus pinaster* mixed stands; CN: *C. arizonica* and *P. nigra* mixed stands; CS: *C. arizonica* and *P. sylvestris* mixed stands. T: Mean temperature; P: Total precipitation; Au: Autumn; Wi: Winter; Sp: Spring; Su: Summer. R^2: Regression coefficient.

while the growth of *P. sylvestris* was related to winter and spring temperatures and precipitations. Overall, while the growth of pine species was mainly related to precipitations and winter and spring temperatures, the climatic factors controlling *C. arizonica* growth differed between mixed forest types.

Growth stability to drought events

Mean resistance (± SE) was 0.841 ± 0.036 indicating that growth was reduced during the drought event around 15% compared to pre-drought growth with non-significant differences between species (Fig. 2). Even though study species showed significantly higher growth rates after than during the drought event (mean recovery was 1.443 ± 0.080), not all species recover pre-drought growth levels. In this regard, *P. pinaster* and *P. sylvestris* showed resilience indices lower than 1 (0.962 ± 0.007 and 0.909 ± 0.004, Fig. 3). We found a significant species-specific effect on recovery and resilience indices in CS and CP stands, respectively (Suppl. material 1: table S4). *C. arizonica* showed higher recovery than *P. sylvestris* and higher resilience than *P. pinaster* (Fig. 2). In addition, larger trees showed lower resistance and resilience to drought in CN stands (Suppl. material 1: table S4).

Forecast growth trends

Growth models projected contrasting growth trends over the 21st century in response to climate scenarios for studied species (Figs 3, 4, 5). Overall, *C. arizonica* showed positive to neutral (i.e. non-significant slopes) growth trends, while native pine species showed neutral to negative trends over the projected periods (Suppl. material 1: table S5). Differences in growth trends between the exotic and the native species were more evident under the RCP8.5 scenario. In CP stands, *P. pinaster* showed negative growth trends during the second part of the 21st century under the RCP2.6 scenario and during the whole projected period under the RCP8.5 scenario, while *C. arizonica* showed positive and neutral growth trends (Fig. 3). In CN stands, *C. arizonica* and *P. nigra* showed similar growth rates under the

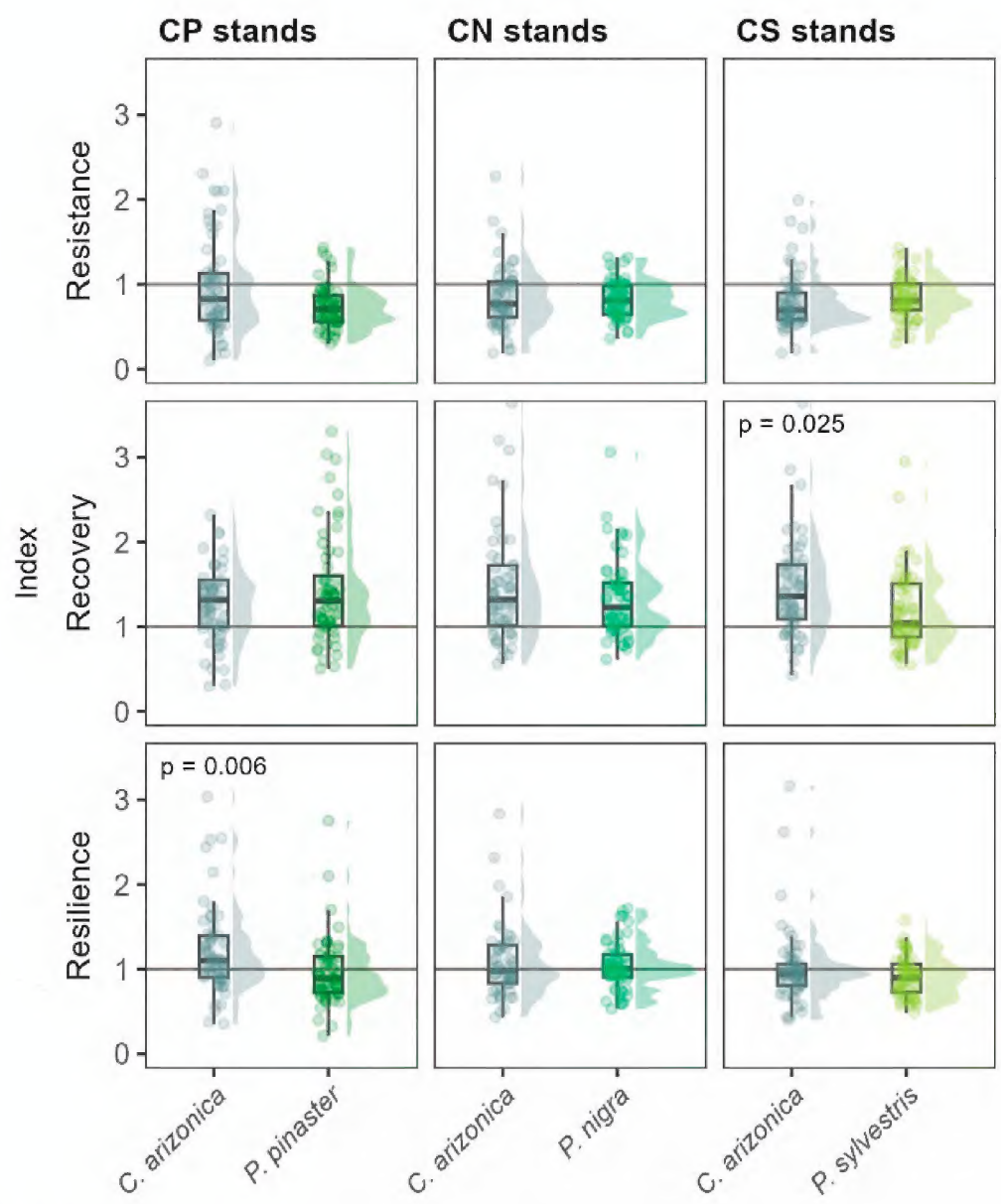

Figure 2. Boxplots of growth resistance, recovery and resilience indices to drought events over the period 1974–2018 for each mixed forest type and species. P-values show significant differences between species. Ca: *Cupressus arizonica*; Pp: *Pinus pinaster*; Pn: *Pinus nigra*; Ps: *Pinus sylvestris*. CP: *Cupressus arizonica* and *Pinus pinaster* mixed stands; CN: *C. arizonica* and *P. nigra* mixed stands; CS: *C. arizonica* and *P. sylvestris* mixed stands.

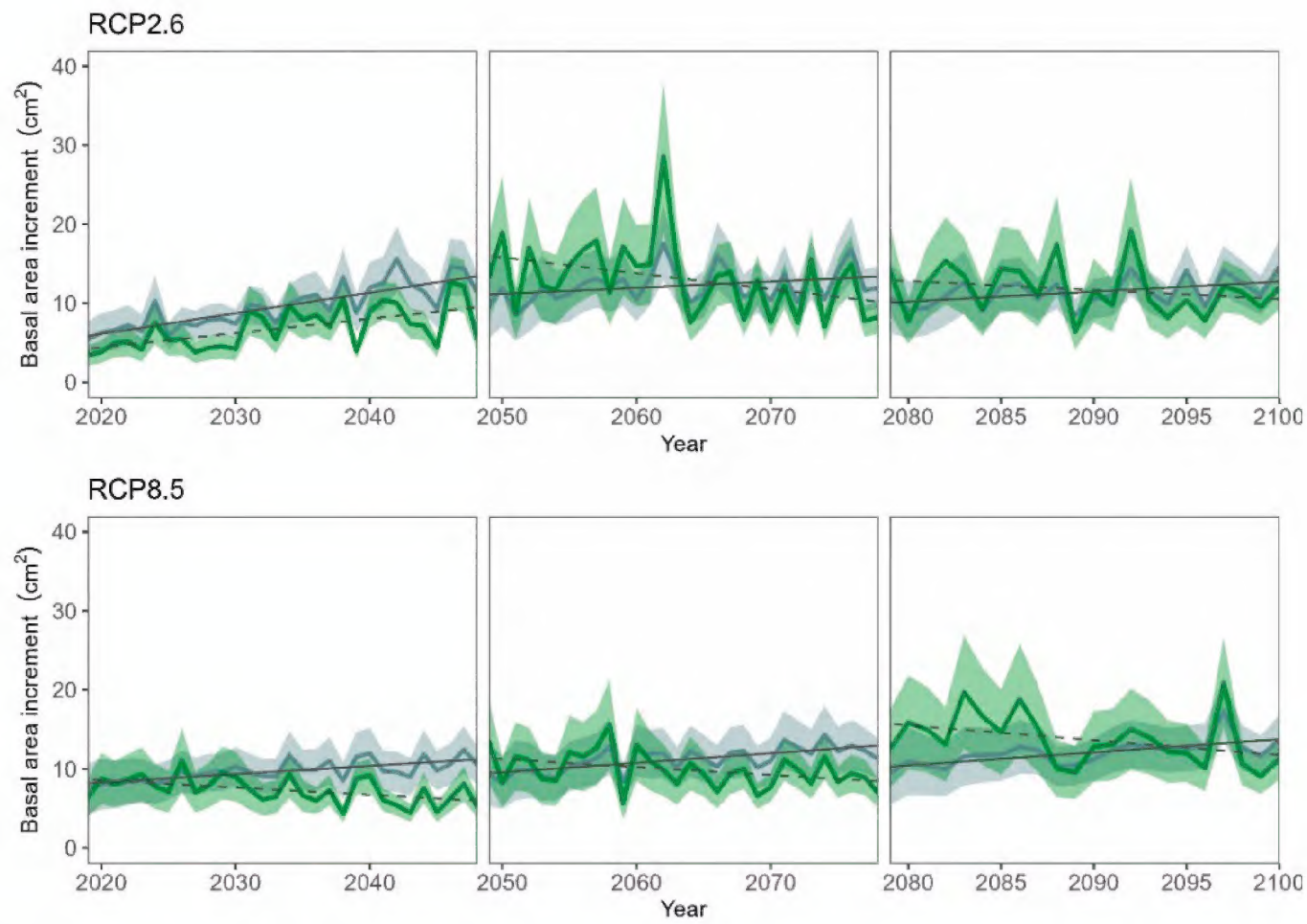

Figure 3. Mean predicted basal area increment (BAI) (± 95% confidence interval) over the projected period (2019–2100) for *C. arizonica* (grey) and *P. pinaster* (green) mixed forest under forcing scenarios RCP2.6 and RCP8.5. Solid and dashed black lines represent growth trends for *C. arizonica* and *P. pinaster*, respectively.

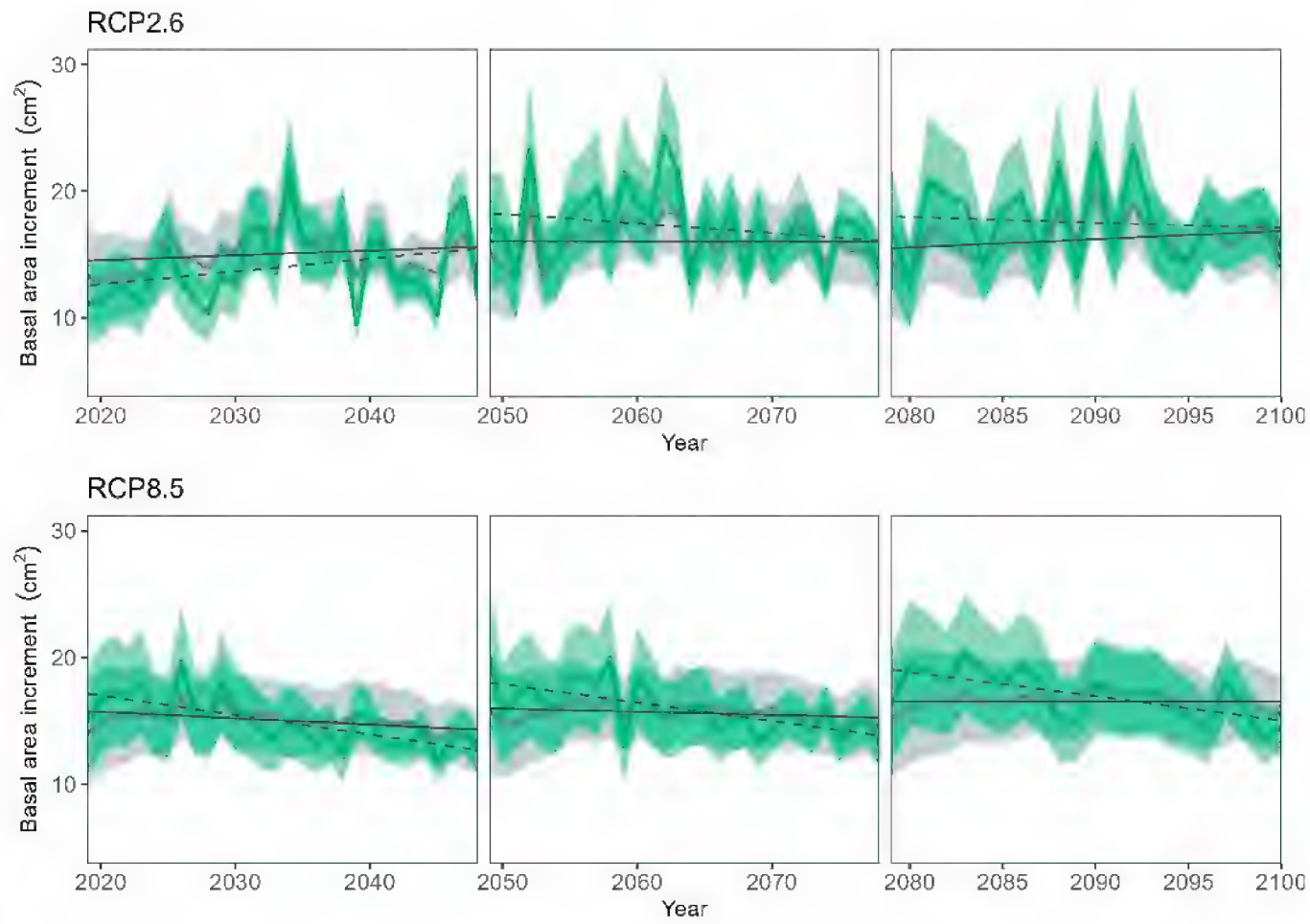

Figure 4. Mean predicted basal area increment (BAI) (± 95% confidence interval) over the projected period (2019–2100) for *C. arizonica* (grey) and *P. nigra* (green) mixed forest under forcing scenarios RCP2.6 and RCP8.5. Solid and dashed black lines represent growth trends for *C. arizonica* and *P. nigra*, respectively.

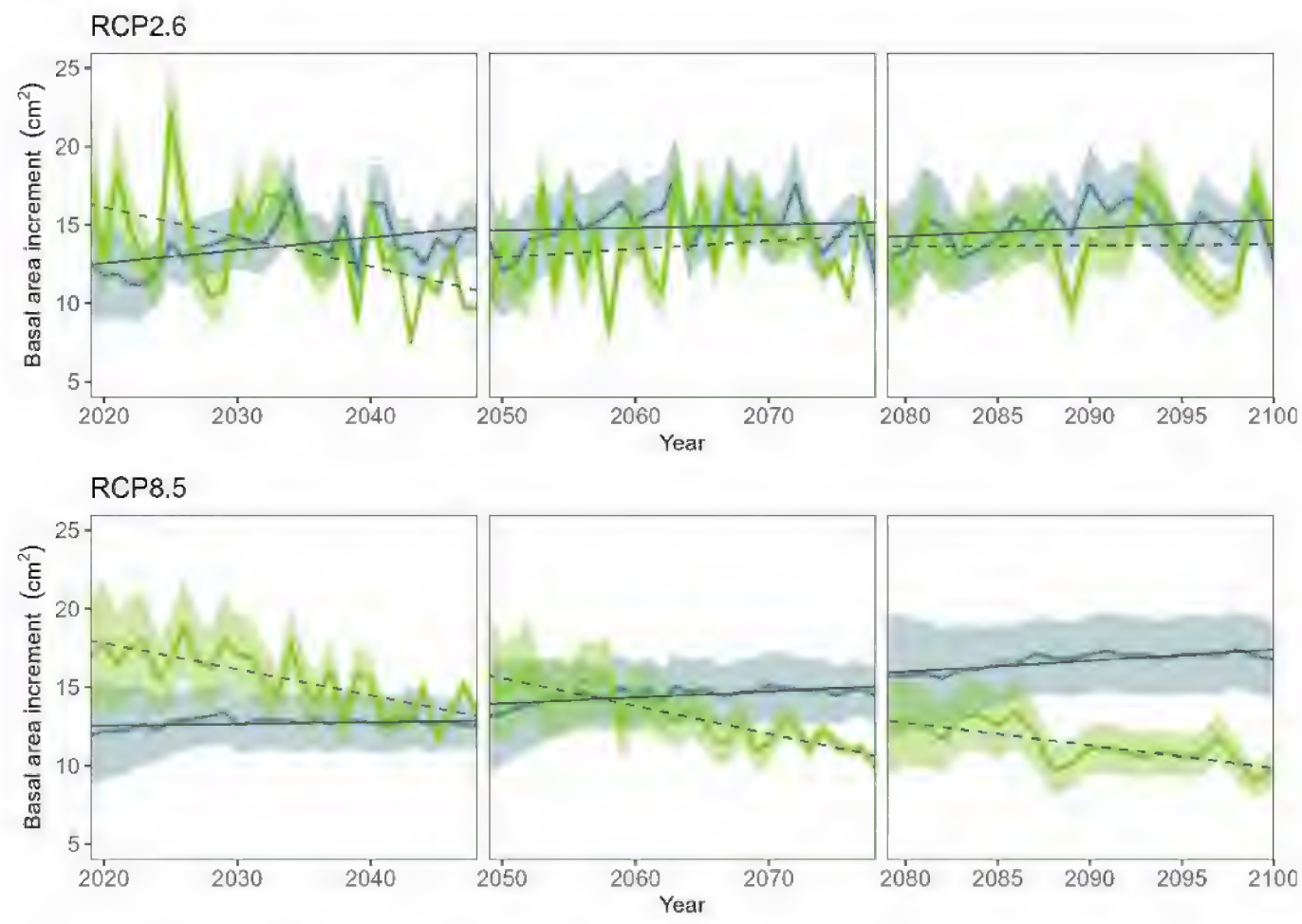

Figure 5. Mean predicted basal area increment (BAI) (± 95% confidence interval) over the projected period (2019–2100) for *C. arizonica* (grey) and *P. sylvestris* (green) mixed forest under forcing scenarios RCP2.6 and RCP8.5. Solid and dashed black lines represent growth trends for *C. arizonica* and *P. sylvestris*, respectively.

RCP2.6 scenario, but the native species showed negative trends while the exotic showed neutral ones under the RCP8.5 scenario (Fig. 4). Similarly, in CS stands, *P. sylvestris* showed negative growth trends under the RCP8.5 scenario, while *C. arizonica* showed neutral and positive responses (Fig. 5).

Discussion

Our assessment of tree performance shows that *Cupressus arizonica* has some advantages in growth, regeneration and survival over co-occurring native pine species. However, these advantages are species- and altitude-specific. Our results suggest that *C. arizonica* could outcompete drought-prone *Pinus sylvestris* at high elevations thanks to its lower climate sensitivity (Table 1), better growth adaptation to future climate (Fig. 5), higher growth recovery after extreme droughts (Fig. 2), higher regeneration capacity and lower mortality. At high elevations, however, *P. nigra* showed higher regeneration and similar growth resistance to extreme droughts than *C. arizonica* (Fig. 2), but negative growth trend under the RCP8.5 climate change scenario (Fig. 4). At low elevations, *P. pinaster* showed higher climate sensitivity (Table 1), negative growth responses to future climate (Fig. 3) and lower resilience than *C. arizonica* (Fig. 2). Thus, native-exotic dynamics at the study site would depend on the balance between different aspects of demographic rates and the magnitude of climate change. Yet, the generally higher performance showed by *C. arizonica* under different climate scenarios suggests that *C. arizonica* has the potential to displace native *P. sylvestris* and *P. pinaster* at high and low elevations, respectively, which point to the invasive potential of this exotic species.

Exotic species need to overcome different barriers to establish, naturalize and finally invade an ecosystem (Richardson et al. 2000). Our study relies on a wide evaluation of the performance (past, present and future) of the exotic *C. arizonica* in Mediterranean mountain forests co-occurring with different dominant pine species. The invasive potential of exotic species is usually assessed comparing different features between native and exotic species under common conditions (Richards et al. 2006; Castro-Díez et al. 2014; Leal et al. 2021). Higher growth rate is considered a trait promoting invasiveness, following the ideal weed hypothesis (Catford et al. 2009; Porté et al. 2012). However, the growth of exotic species can be attenuated when co-occurring with native species (Kawaletz et al. 2013). Our results showed no differences in average radial growth between exotic *C. arizonica* and co-occurring native pines, in contrast to previous studies comparing exotic and native trees (Rojas-Badilla et al. 2017), but in consonance with the lack of differences in growth between phylogenetically close native and introduced pine species in Central Europe (Klisz et al. 2023) and between exotic- and native-dominated stands in Mediterranean Spain (Lázaro-Lobo et al. 2023).

Nevertheless, *C. arizonica* showed some advantages in radial growth over native pine species. *C. arizonica* is considered a species well-adapted to drought (Harrington et al. 2005; Pool et al. 2013), which could favour its future persistence and spread in the study area under increased aridity. Our results support a lower growth sensitivity of the exotic species to climate than in its native counterparts. First, the number of climatic factors affecting growth are less than in native species and, overall, showed lower coefficients in the growth model, reflecting the high environmental tolerance of this exotic species (Rejmánek and Richardson 1996; Goodwin et al. 1999). Tree growth of study pine species increased with winter temperatures and winter and spring precipitation. However, at the dry edge of pine species distribution, warming can reduce tree growth by increasing water stress in late spring and early summer (Camarero et al. 2015; Marqués et al. 2018; Díaz-Martínez et al. 2023). This might be the case of *P. sylvestris*, which is considered the most vulnerable of the study pine species to drought (Galiano et al. 2010; Herrero et al. 2013;

Herrero et al. 2023) and showed a negative growth response to higher spring temperatures in our study area. Second, growth predictions in the worst greenhouse gas scenario favours the growth of the exotic species, with native pines showing negative growth trends. Previous studies comparing radial growth between native and exotic species did not find that future conditions could benefit exotic over the native species under more humid conditions (González-Muñoz et al. 2014), which suggests that differences in species' performance can be aggravated in water-limited ecosystems. In fact, annual precipitation in our study site was higher as compared to that in the native range of *C. arizonica* (e.g. southeast Arizona, Parker (1980a), https://es.climate-data.org). Finally, *C. arizonica* showed higher recovery from extreme droughts than *P. sylvestris* at high elevation and higher resilience than *P. pinaster* at low elevation. Small differences in resilience capacity to extreme droughts could increase the competitive ability of *C. arizonica* due to the expected increases in frequency and severity of extreme climatic events (IPCC 2023).

Besides radial growth, *C. arizonica* showed some advantages in other demographic variables. In fact, the exotic species showed higher regeneration capacity than *P. pinaster* at low elevations and *P. sylvestris* at high ones. This could be due to the higher tolerance of young seedlings to shade and drought compared to native pines (Parker 1980b; Pool et al. 2013). Although *C. arizonica* regeneration is associated with disturbances that increase light and remove litter, this species can also tolerate shaded conditions of forest understorey for long-time periods (Parker 1980b). This could represent a benefit in comparison to light-demanding pine saplings (Barbéro et al. 1998). *C. arizonica* could create a soil seed bank and, thus, take advantage of forest gaps created by disturbances. Both species, *P. sylvestris* and *C. arizonica*, regenerate well after wildfires (Parker 1980b; Spînu et al. 2020), but we observed massive regeneration of the exotic species in burnt areas within the study site. This could be advantageous for *C. arizonica* under climate change scenarios, in which a higher risk of wildfire occurrence is expected (Turco et al. 2018; Dupuy et al. 2020), especially in forests with high tree density and low structural heterogeneity (Stephens et al. 2010). In addition, the exotic *C. arizonica* was the only species showing no mortality in the study area. This could provide an advantage for *C. arizonica*, not only due to higher survival rate, because also its understorey seedlings could take advantage of forests gaps and release of resources created by dead trees. However, the competitiveness seems to be greater in the case of Mediterranean *P. nigra* (with higher regeneration capacity than *C. arizonica* and similar resilience to extreme droughts) than in boreo-alpine *P. sylvestris*. In addition, other native species, such as *Q. ilex* and *J. communis*, showed higher regeneration density in the area, which also suggests that drought tolerant and resprouting species can be favoured in the future.

Considering all the results together, the future displacement of native pines by the exotic *C. arizonica*, which is more tolerant to drought, seems plausible. At present, the exotic *C. arizonica* is considered a naturalised species in the Iberian Peninsula (Sanz Elorza et al. 2004), but it is likely that *C. arizonica* has not completely overcome abiotic and biotic barriers to successfully invade Iberian Mediterranean ecosystems (Richardson et al. 2000). Many studies of invasive plants have suggested that a "lag" time is a common feature in their population dynamics (Crooks 2005). In the study area, *C. arizonica* can be in a lag time, typically defined as a period of several years to several decades between the introduction and establishment of a species and its period of rapid geographic range expansion (invasion) (Kowarik 1995). Changes in the climate that favour *C. arizonica* over the pines could surely break this lag time.

If *C. arizonica* finally outcompetes native pine species, it could increase the size of its populations and increase its distribution area. This could boost its invasive potential and increase the chances of expanding to surrounding areas. If so, the species would move from the lag phase to the log phase or period of exponential population growth, reproduction and expansion, where management actions to reduce populations of the invasive species are less efficient and more expensive. It is important to note that, for exotic trees introduced to Europe, the average lag time is estimated at 170 years (Kowarik 1995) and that *C. arizonica* was used for afforestation in Spain during the mid-20th century. Thus, it is likely that this exotic species will be close to the end of its lag time period by the end of this century, when expected climatic conditions might increase its dominance over native species in the area. In this context, the current implementation of management actions orientated to reduce the populations of this exotic species would play a key role in controlling its invasive potential.

Conclusions

Our results present for the first time an evaluation of the invasive potential of the exotic *C. arizonica* in Mediterranean forests that integrates species' demographic rates and responses to climatic extreme and climate change scenarios. *Cupressus arizonica* showed less growth dependence to climatic variability, lower mortality and more regeneration than native pine species, which favours the naturalisation of the species and increase the probability of invasion in the study area. Climate change can also favour the invasive potential of this species by hindering the development of native ones. Compared to *P. pinaster* and *P. sylvestris*, *C. arizonica* had greater growth recovery and resilience to drought events, which gives the exotic competitive advantages over the pine species in the context of increased aridity. In addition, our forecast models stressed that *C. arizonica* may be more favoured by warmer and drier conditions in the future than native pines, which showed negative growth trends and, thus, higher vulnerability. Therefore, we recommend implementing actions to control this exotic species that can break its lag time and invade Mediterranean forest ecosystems in the near future.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualisation: EPC, AH and EA; Investigation: EA, AH, NCM and VCA; Formal analysis and visualisation: EA and VCA; Writing – original draft: SMV and EA: Writing – review & editing: all. Funding acquisition: EA and EPC.

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Data availability

The data underpinning the analysis reported in this paper are deposited at https://dx.doi.org/10.6084/m9.figshare.24680160.

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Supplementary material 1

Can exotic tree species outcompete native ones in Mediterranean mixed forests under climate change

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